noted that the ridges appeared most clearly when sections were cut longitudinally through each mitochondrion and that they were oriented "more or less perpendicular to the long axis of the mitochondrion" (p. 432). He observed that the ridges have a "trilaminar structure" with "a central layer 8 to 10 mμ thick" surrounded by two thinner and denser layers. He called these ridges or protrusions "cristae mitochondriales" (p. 433) and, although noting that their appearance varied between cell types, concluded that they were likely to be regular features of mitochondria. He even suggested that they could serve as a "criterion for the identification of mitochondria in electron microscopy where the characteristic staining reactions of these organelles are of no avail" (p. 438).

By differentiating the cristae from the fluid matrix within the interior of the mitochondrion, Palade offered a structural decomposition that raised the prospect of advancing the mechanistic account of mitochondrial function by localizing different biochemical operations in different structural components. Palade himself put forward the suggestion that the aerobic oxidation reactions were directly tied to the structure of the mitochondrion, especially the cristae:

> It is well established that isolated mitochondria are able to carry out *in vitro* complicated oxidative processes that imply the action of a considerable number of enzymes. As these oxidations are apparently well co-ordinated and, in addition are dependent on the morphological integrity of the mitochondria . . . , it has been postulated that the enzymes involved in such processes are maintained in a 'definite spatial relationship' (Schneider & Hogeboom, '51) inside the organelles. It may be assumed that they are arranged in the proper order in linear series or chains – a disposition comparable in design and efficiency to an industrial assembly line. Such enzymatic chains have to be built at least partially in the solid framework of the mitochondrion because some of the component enzymes, namely succinic acid dehydrogenase (succinoxydase) and cytochrome *c* oxydase, are known to be insoluble and structure-bound. If we integrate the present morphological information with what is known from the general behavior of the mitochondria (e.g., their flexibility, response to variations in osmotic pressure and results obtained by centrifuging disintegrated organelles), it may reasonably be assumed that the mitochondrial matrix is fluid and that the membrane and the ridges represent the solid framework. In the present state of our knowledge, the internal ridges of the mitochondria appear as the most probable location for the postulated enzyme chains. (pp. 438–9)[11]

[11] In a footnote, Palade commented on Green's proposal of a cyclophorase system: "The work referred to deals with some dehydrogenases of the 'cyclophorase system,' a tissue residue